Predicting habitat use by ringed seals (*Phoca hispida*) in a warming Arctic

Carla Freitas[a,b,*], *Kit M. Kovacs*[a], *Rolf A. Ims*[b], *Christian Lydersen*[a]

[a] *Norwegian Polar Institute, Polar Environmental Centre, Tromsø N-9296, Norway*
[b] *Institute of Biology, University of Tromsø, Tromsø N-9037, Norway*

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ABSTRACT

Models predicting the spatial distribution of wild animals are essential for conservation purposes (e.g. conservation plan formulation and reserve selection) and for assessment of ecological impacts of factors such as pollution and climate change. When a species' habitat use depends on highly dynamic environmental conditions, predictive models should be constructed for specific time periods, taking into account the existing spatial distribution of the relevant habitat conditions. In the case of ringed seals (*Phoca hispida*), habitat use is intimately connected with sea ice. In the High Arctic Archipelago of Svalbard, ringed seals have two different tactics for selection of large-scale summer habitat. Some individuals spend summer in coastal (inshore) areas, while others migrate offshore to the southern limits of the northern sea ice edge. The predicted decline of the sea ice extension in the Arctic is likely to critically affect the profitability of this latter foraging-migration tactic. Two modelling approaches were used in this study to explore when impacts are likely to occur. One approach explored small-scale habitat use within the two types of summer areas using habitat residency functions. These functions were empirically derived from statistical Cox proportional hazards (CPH) models fit to spatial data on seal residency times (*i.e.*, first-passage times) and local habitat features such as ice conditions. These functions predict the probability of using a given area longer than a given time. They were subsequently used to produce cartographic predictions of habitat use intensity for different times of the year, under various scenarios for sea ice conditions. Such dynamic predictions of animal space use (in space and time), can have wide applications for studies of other marine and terrestrial species that are based on data collected from telemetry. In the second approach, data from satellite telemetry and ringed seals energetics during summer were combined to construct a model for ringed seal blubber mass gain during summer. This model was then used to predict the profitability of offshore migrations as a function of the distance to the sea ice edge. This distance is expected to increase in a warmer climate. Migrations to offshore ice edges were predicted to become energetically unprofitable for ringed seals if the sea ice retreats further than 600–700 km from Svalbard.

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1. Introduction

Models predicting the spatial distribution of wild species have gained increased attention in recent years. They have been used to explain observed patterns of habitat use (e.g. Hastie et al., 2005; Hayward et al., 2007) and in some cases also to make cartographic predictions of species distribution (e.g. Cañadas et al., 2005; Ferguson et al., 2006). Beyond being useful for understanding the biological requirements of animals, such models can also be of vital importance for conservation purposes, constituting the background frameworks for conservation plans and reserve selection, and for assessment of risks associated with factors that might alter the physical environment in a negative manner, such as climate change for ice-associated species (see Guisan and Thuiller, 2005).

A variety of statistical techniques have been applied to predict habitat distribution (see Guisan and Zimmermann, 2000; Boyce et al., 2002; Manly et al., 2002; Guisan and Thuiller, 2005; Hirzel et al., 2006; Redfern et al., 2006). Generalised Linear Models (GLMs) and their semi-parametric extensions, the Generalised Additive Models (GAMs), are frameworks that have gained increased interest in recent years (see Guisan et al., 2002), especially when analyzing presence/absence data from surveys (e.g. Hastie et al., 2005; Hayward et al., 2007). In telemetry studies, where data on time spent in different habitats can be obtained in addition to presence/absence data, statistical approaches dealing with time-based events can be particularly useful (Fauchald and Tveraa, 2003; Freitas et al., in press). One such statistical framework is the Cox proportional hazards (CPH) model (Cox, 1972), which models the time until an event occurs. CPH models have been used extensively to model survival data in medical research and failure-time data of industrial products (see e.g. Cox and Oakes, 1984; Collett, 2003). These models have also been used in resource selection studies to model the time until a resource (food or habitat) is selected (see examples in Manly et al., 2002, Chapter 6) and to model the risk of leaving particular habitats (Freitas et al., 2008). Recently, it has also been proposed that CPH models could be used to predict habitat use (Freitas et al., 2008a).

In areas where habitat use is influenced by highly dynamic environmental conditions, such as sea ice conditions or sea surface temperatures, predictive models have to cope with the dynamic nature of the predictor variables and therefore must be constructed for specific time periods, taking into account the spatial distribution of the habitat conditions within the selected time frame (see Hobday and Hartmann, 2006).

In the case of ringed seals (*Phoca hispida*), habitat use is intimately connected with sea ice. This seal is a circumpolar arctic ice-breeding species that normally spends winter and spring in areas of annually formed sea ice inside fjords and bays (McLaren, 1958; Lydersen and Gjertz, 1986). Females give birth inside snow-lairs in March–early April; mating takes place about 1 month later (Lydersen, 1998). Following mating, ringed seals use the remaining annual land-fast sea ice (sea ice that makes contact with land) as a platform for moulting (Smith, 1987; Lydersen, 1998). In summer, when the moulting season is over and the coastal, annual sea ice disappears, ringed seals leave the breeding and moulting areas to spend the rest of the year elsewhere. In the arctic archipelago

of Svalbard (Norway) satellite tracking records (Gjertz et al., 2000; Freitas et al., 2008) have shown that ringed seals exhibit two large-scale movement/habitat selection tactics during the summer/early fall. Some seals spread out along the coast of the archipelago (hereafter termed inshore movements), while other seals move offshore to the southern limits of the northern sea ice edge. These latter long-distance movements represent a foraging-migration tactic as they return to coastal areas again (and mix with the inshore seals) before the fjords in the archipelago start to freeze up in the late autumn/early winter (Freitas et al., 2008). Thus, all seals are in place for the coming breeding period and can maintain breathing holes and establish territories when ice formation starts (Freitas et al., 2008).

Ringed seals, especially reproductively active animals, lose considerable amounts of blubber during the energetically demanding breeding and moulting seasons, with the lowest blubber thickness values being recorded in July (Smith, 1987; Ryg et al., 1990). The blubber energy stores are then rebuilt during late summer and autumn through intensive feeding (Ryg et al., 1990), and not surprisingly, ringed seals concentrate their foraging time in productive areas such as glacier fronts and the offshore marginal ice zone at this time of the year (Freitas et al., 2008).

The speed and directionality of the movements of migrating ringed seals in Svalbard suggests that they do not spend any time foraging while in transit to the northern ice (Freitas et al., 2008). The high concentrations of food at the ice edge (see Engelsen et al., 2002) probably make it unprofitable in terms of energy gain to stop and search for food patches along the way. This also implies that the distance to the ice-edge feeding ground is an important factor in the ringed seals' annual energy budget. The summer sea ice extent has been retreating northwards as a function of global warming (Comiso, 2002; Comiso et al., 2008; Stroeve et al., 2005, 2007; Francis and Hunter, 2006; Christensen et al., 2007). Thus, it is likely that a point will be reached where the energetic costs for the seals of travelling to the edge will be so high that it is not energetically profitable to conduct this long feeding migration.

The overall aim of the present study is to predict habitat use by ringed seals in the waters around Svalbard for different periods of the year and under various scenarios of sea ice conditions. Two modelling approaches are used. In the first we derive predictions of ringed seal spatial distributions based on residency time functions derived from CPH models with local habitat features as predictors. These predictions are made for the two major summer areas (*i.e.* coastal waters of Svalbard and offshore sea ice edge). In the other approach we model the energetic profitability of the migration tactic, considering future scenario with a northward receding summer ice edge.

2. Methodology

2.1. Predicting habitat use intensities

In July 2002 and 2003, 22 adult and sub-adult ringed seals were equipped with satellite-relayed data loggers (SRDLs) in Svalbard, Norway (approximately 78°70′N, 20° 25′E). Capture

and tagging methods are described in Lydersen et al. (2004). The SRDLs provided location data using the Argos System (Toulouse, France); Argos accuracies range from <350 m to >1000 m (Argos, 1996). Using first-passage times (FPT, Fauchald and Tveraa, 2003) as CPH model survival times, Freitas et al. (2008) modelled the effect of a set of environmental conditions on FPTs. Models were built using location data collected between July and December 2002 and 2003. CPH model selection and inferences about small-scale habitat selection are described and discussed in Freitas et al. (2008); here we summarize only what is needed for the present modelling study. For inshore seals in coastal waters, FPTs were affected mainly by distance to glaciers, but also by water depth, distance to the coast and time of the year (see model coefficients in Table A1). For seals that travelled to offshore waters during summer ($n = 9$ seals, 11 trips), FPTs were mostly affected by sea ice concentrations and to a lesser degree by distance to the tagging location (depending on ice concentrations and time of the year) and by time of the year (see Freitas et al., 2008). Using these CPH models (the inshore model and a modification of the offshore model; see below), survival functions $\hat{S}_i(t)$ were estimated in the present study for a set of new locations (areas), in order to predict habitat use in those areas for different times of the year and under various scenarios of sea ice conditions. The general CPH model is written as:

$$h(t) = \exp(\beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_p X_p) h_0(t), \tag{1}$$

where $h(t)$ is the hazard function, *i.e.* the risk that an event will occur at time t. In the present context it represents the risk that an animal will leave an area at time t. X_1, X_2, ..., X_p are the explanatory variables in the model, and β_1, β_2, ..., β_p are the coefficients that describe the contribution of these variables. $h_0(t)$ is the baseline hazard function at time t, *i.e.*, the risk of leaving an area when all explanatory variables are equal to zero or to a defined base value. This baseline hazard function $h_0(t)$ is estimated from the β coefficients, while the β coefficients, which are the unknown parameters in the model, are estimated using the method of maximum likelihood (see Collett, 2003). Once β coefficients are estimated from Eq. (1), survival functions, which describe the probability of being in an area longer than a time t, can be obtained. The estimated survival function for a given ith area is given by:

$$\hat{S}_i(t) = (\hat{S}_0(t))^{\exp(\hat{\beta}' \mathbf{x}_i)}, \tag{2}$$

where $\mathbf{x}_i$ is the vector of values of the explanatory variables for the ith area, $\hat{\beta}$ is the vector of estimated coefficients (from Eq. (1)) and $\hat{S}_0(t)$ is the baseline survivor function (see Collett, 2003, pages 98–99 for details on the estimation of $\hat{S}_0(t)$). Since $\hat{S}_i(t)$ predicts the probability of using an area longer than a time t under a given set of variables $\mathbf{x}_i$, it can be used as a predictive measure of habitat-use intensity.

Predictions were made separately using inshore and offshore CPH models. CPH models for inshore waters were fitted using FPTs at the scale (r) of 10 km radius, since this was the spatial scale at which seals performed their "Area Restricted

Search" behavior in inshore waters (see Freitas et al., 2008). Predictions for inshore waters were therefore also made at that scale, meaning that the resulting survival function $\hat{S}_i(t)$, will predict the probability of using the surrounding 10 km for longer than a given time t. CPH models for offshore waters were fitted for a spatial scale of 30 km (Freitas et al., 2008), and therefore survival functions $\hat{S}_i(t)$ in those areas correspond to the probability of using the surrounding 30 km for longer than a given time t. In order to make comparison between inshore and offshore areas possible, CPH models and corresponding survival functions $\hat{S}_i(t)$ in inshore waters were also fitted using a scale of 30 km (Table A2). The CPH model for offshore areas was fitted without the variable "distance to the tagging location" and therefore assumes that trips can start from anywhere in Svalbard. Note that this variable alone did not significantly affect ringed seals FPTs (see Freitas et al., 2008). For simplification, the offshore model also presents time of the year as monthly intervals (see Table A3), instead of the 7 days intervals used in the original model in Freitas et al. (2008). These modifications of the original CPH model reduced the percentage of variability explained by the model from 58.1% to 29.6%. However, the new model has a more general application suitable for predictive purposes (while the original, more detailed model was more appropriate for explaining the observed habitat use patterns).

In order to estimate the expected survival functions $\hat{S}_i(t)$, or in this context FPT functions, for a set of new areas, a grid with a cell size of 2.5 km was created for the area of interest (Svalbard Archipelago). This grid cell size was chosen as a compromise between computer processing time and resolution of the output (prediction maps). Physical variables used in the inshore and offshore CPH models were obtained for the central point of each grid cell i. These variables were: depth; distance to shore; distance to the nearest glacier front; and sea ice concentration. Depths were extracted from 2.5 km resolution grid data from IBCAO (International Bathymetric Chart of the Arctic Ocean, Version 1.0, 2001). Distances to the coast and to the nearest glacier front (around land when appropriate) were measured using Norwegian Polar Institute digital maps (updated using aerial photographs of glacier fronts and coastlines taken from 1993 to 1998). Only coastal glacier fronts (*i.e.* glaciers in direct contact with the ocean) were included in the analyses. Sea ice concentrations were also obtained for each grid cell i, but since this variable is highly dynamic, three scenarios were used: the sea ice concentrations observed in August 25th of 2002, 2003 and 2004. Sea ice distributions on these dates were approximately the minimum summer sea ice extent. Sea ice concentrations were extracted from daily 10 km resolution data from OSI-SAF (The Ocean & Sea Ice Satellite Application Facility, http://www.osi-saf.org).

Using the above environmental variables for each cell i as new values for the explanatory variables in the predictions, a survival function $\hat{S}_i(t)$ was then estimated for those cells. The probability of being in the area surrounding the ith cell (in the r km radius) longer than 24 h ($\hat{S}_i(24)$) was extracted from each survival function $\hat{S}_i(t)$ and plotted on a map, in order to generate a cartographic prediction of habitat use intensities for those areas. CPH models and survival functions $S(t)$ were estimated using R software (package survival). R is distributed

Table 1 – Summary of the parameters used in the blubber mass gain model			
Parameter	Value	Description	Source
DailyGainCoast	0.361	Blubber mass gain at the coast (kg/day)	Ryg et al. (1990)
FMR	2 (70 BodyMass$^{0.75}$ × 4.187/1000)	Field metabolic rate (MJ/day), which represents the daily energy loss	Kleiber (1975)
DailyLoss	FMR/39.33	Daily energy loss in kg of blubber (kg/day)	Costa (1987)
Speed	60.3	Average travelling speed (km/day)	This study (Table 2)
ExtraGainIce	0.277[a]	Extra mass gain at the ice (kg/day) compared to the coast	This study, using a coastal blubber mass gain of 0.361 kg/day and assuming that seals returned to Svalbard at the same condition as if they would have stayed at the coast
Miminum start date	July 22nd	Minimum start date of offshore trips	This study (Table 2)
Mean start date	July 31st	Mean start date of offshore trips	This study (Table 2)
Maximum start date	August 23rd	Maximum start date of offshore trips	This study (Table 2)
Maximum trip duration	90	Maximum number of days available to perform offshore trips	Value found assuming that seals have to be back in Svalbard before sea ice forms at the coast (see Freitas et al., 2008), taking into consideration the observed minimum start date of the offshore trips (Table 2) and the time of sea ice formation in Svalbard (observed from OSI-SAF sea ice concentration satellite imagery data 2002–2005)

[a] Value assumed constant for all season in scenario (a) and assumed to decrease from day 60 in scenario (b).

under the GNU General Public License (R Development Core Team, 2007).

2.2. Predicting energetics of offshore migrations: modelling blubber mass gain

Energy gain, in terms of lipid mass gain (in the blubber layer), in summer and autumn, was modelled both for ringed seals that remained coastal throughout the year, and for ringed seals that travelled to the northern ice edge, located at simulated distances from the Svalbard Archipelago.

Freitas et al. (2008) showed that the ringed seals that travelled offshore initiated these trips during late July with the earliest departure taking place on July 22nd. The same study also showed that most seals returned to Svalbard when the coastal waters were still ice free, probably in order to be resident within the breeding areas in time to maintain breathing holes when the fjords start to freeze (Freitas et al., 2008). In the years 2002–2005 sea ice formation in Svalbard took place during mid-late October (OSI-SAF satellite imagery sea ice data, http://www.osi-saf.org). This simulation therefore considers that the seals have 90 days (from late July to late October) available to replenish their blubber stores; they can do this coastally, or by travelling to the sea

ice edge for a variable number of days. Parameters used in the simulations are summarised in Table 1 and are described below.

2.2.1. Blubber mass gain at the coast
According to Ryg et al. (1990), ringed seals collected in Svalbard have a mean blubber mass gain of 0.361 kg per day from July to September (data merged for males ($n = 4$) and females ($n = 3$); see Ryg et al., 1990). In the model we assume that this deposition rate continues until the end of the modelling period (October). This means that at the end of the simulation period (90 days) seals that stay at the coast will have gained a total of 32.5 kg of blubber mass.

2.2.2. Blubber mass lost in transit
The behavior of the satellite-tracked animals (swimming speed and directionality of their trips; see Freitas et al., 2008; Table 2) indicates that ringed seals probably do not forage while travelling towards the ice, which seems reasonable since productivity in these pelagic ice-free waters is known to be low (Engelsen et al., 2002). Accordingly, we assume in the model no energy intake during transit. Further, we assume that seals have a Field Metabolic Rate (FMR) of 2 times Basal Metabolic Rate (BMR, according to Kleiber, 1975), similar to many marine mammal energetics studies (e.g. Hammill and Stenson, 2000;

Table 2 – Summary of the offshore trips performed by ringed seals equipped with satellite-relayed data loggers in Svalbard in 2002 and 2003									
Reference	Sex	Body mass (kg)	Trip no.	Start date	End date	Trip duration (days)	Total travelling distance[a] (km)	Total travelling time[a] (days)	Average speed (km/day)
F31_2002	F	31	1	22 July 02	29 August 2002	38	485	13.2	36.7
F33_2002	F	33	1	26 July 02	06 September 2002	42	550	9.9	55.5
F36_2002	F	36	1	29 July 02	02 September 2002	35	630	10.8	58.6
F37_2002	F	37	1	23 August 02	21 November 2002	90	515	11.3	45.8
F57_2002	F	57	1	01 August 02	01 September 2002	31	721	11.5	62.9
F59_2002	F	59	1	01 August 02	25 August 2002	24	163	3.0	54.0
F59_2002	F	59	2	15 September 2002	30 September 2002[b]	15 +	240	3.2	74.8
M50_2002	M	50	1	23 July 2002	20 October 2002[b]	89 +	449	7.0	64.2
F34_2003	F	34	1	24 July 2003	11 August 2003	18	107	1.3	84.8
F34_2003	F	59	2	18 August 2003	08 September 2003	21	522	9.1	57.2
F37_2003	F	37	1	07 August 2003	18 September 2003	42	427	6.2	69.2
Mean				31 July[c]	9 September	37.9	437.2	7.9	60.3
S.E.				3.3 days	9.7 days	7.1	57.9	1.2	4.0

Trips were performed by 9 out of 22 animals (13 stayed near the coast throughout the tracking period). Trip no. refers to the trip number.

[a] To and from the ice edge.

[b] Contact with the seal was lost before it returned to the coast. Total travelling distance and total travelling time for these animals therefore only includes the trip to the sea ice edge.

[c] Mean start date of first trip.

Nilssen et al., 2000; Carlini et al., 2005) and within the normal range measured in field and captive studies (Coltman et al., 1998; Sparling and Fedak, 2004; Sparling et al., 2008). In addition, we assume that all mass lost during transit is derived from lipids in the blubber layer (with a caloric density of 39.33 kJ/g). According to these assumptions a 60 kg ringed seal would lose 0.321 kg per day during transit.

2.2.3. Blubber mass gain at the ice edge

In the model, we further assume that the ringed seals that travel to the ice edge are in the same condition upon return as those seals that stayed in coastal areas. This implies that the seals travelling to the ice edge must compensate for the mass lost during transit with increased mass gain during the period they spend at the ice edge. This extra mass gain was calculated to be 0.277 ± 0.052 kg per day (mean $\pm$ S.E.) spread over the foraging phase, based on transit times and at-the-edge times calculated from tracking data for ringed seals from 2002 and 2003 (Table 2). The transit times and corresponding extra mass gains are based on data from 7 seals (8 trips) for which tracking records were available for the complete trip and that returned to the coast in August and September (see Table 2).

Ringed seals foraging at the ice edge feed primarily on polar cod (*Boreogadus saida*), even when other potential prey species are more abundant (Wathne et al., 2000). The polar cod themselves feed mainly on sympagic amphipods and pelagic copepods (Lønne and Gulliksen, 1989; Scott et al., 1999). These prey organisms decrease markedly in abundance in the autumn (from late September onwards; Werner and Gradinger, 2002). Such decreases are expected to affect upper trophic levels, although the time-lag to an effect (if one occurs) on ringed seals is unknown. In order to account for this potential reduction in food availability late in the season, we modelled blubber mass gain for ringed seals that travelled to the ice edge both (*a*) assuming constant blubber mass throughout the whole season and (*b*) assuming a logistic decrease in blubber mass gain in the autumn.

(a) *Constant blubber mass gain*
    For constant blubber mass gain, the total extra daily blubber deposited at the ice edge (ExtraGainIce) can be calculated simply as:

$$\text{ExtraGainIce (kg)} = 0.277 \times \text{DaysIce} \quad (3)$$

   where 0.277 is the average extra blubber mass gain per day (kg) and DaysIce is the number of days at the ice edge.

(b) *Logistic decrease in blubber mass gain*
    In this case, blubber mass gain at the ice was assumed to decrease from day 60 to day 80, to one third of its initial value (0.277/3). Such a decrease can be modelled using a logistic function with slope -0.3 and t_{50} (day at which the reduction is at 50%) equal to day 70. From this logistic curve, the extra blubber mass gain at time t is given by the following relationship:

$$\text{ExtraGainIce}_t \text{ (kg)} = \frac{0.277}{1 - \text{prop}} \times \left(\frac{1}{1 + \exp(a(t_{50} - t))} - \text{prop} \right) \quad (4)$$

where 0.277 is the initial blubber mass gain value, a is the slope of the curve (-0.3) and prop is -0.5, the adjustment value to make the final value equal to one third of the initial value.

The total extra blubber mass gained during a period t_1 to t_2 will be given by:

$$\text{ExtraGainIce (kg)} = \int_{t_1}^{t_2} \left(\frac{0.277}{1 - \text{prop}} \right.$$
$$\left. \times \left(\frac{1}{1 + \exp(a(t_{50} - t))} - \text{prop} \right) \right) dt \quad (5)$$

After integrating Eq. (5) and taking into account that $t_2 = t_1 + t_{ice}$ (initial time t_1 plus the time spent in the ice t_{ice}), the upper formula can be presented as:

$$\text{ExtraGainIce (kg)} = \frac{0.277}{1 - \text{prop}} \times (t_{ice} \times (1 - \text{prop})$$
$$- \frac{1}{a} \times \ln \left(\frac{1 + \exp(a \times t_{50} - a \times t_1)}{1 + \exp(a \times t_{50} - a \times t_1 - a \times t_{ice})} \right))$$
$$(6)$$

2.2.4. Total blubber mass gain

The total blubber mass gain (TotalGain) during the total simulation period (TotalTime) was calculated as:

$$\text{TotalGain (kg)} = \text{DailyGainCoast} \times (\text{TotalTime} - \text{DaysTransit})$$
$$+ \text{ExtraGainIce} - \text{DailyLoss} \times \text{DaysTransit}$$
$$(7)$$

where DailyGainCoast is the daily mass gain at the coast (0.361 kg), TotalTime the total number of days (90) and DaysTransit is the number of days in transit. This number is given by $2 \times \text{Dist/Speed}$, where Dist is the distance to the ice edge and Speed is the mean speed in transit to the ice edge, estimated to be 60.3 ± 4.0 km/day (mean $\pm$ S.E.) from the tracking data (Table 2). ExtraGainIce is the extra blubber mass gain in the time period that the seal is at the ice edge (calculated using Eqs. (3) or (6) depending on the scenario being modelled). DailyLoss is the daily blubber mass loss in transit (FMR/39.33; see section 2.2.2).

Simulations were carried out using a 60 kg ringed seal leaving Svalbard at various dates: at day 1 (July 22nd), at day 10 (July 31st) and at day 33 (August 23rd)—which represents the first, the average and last day that the tracked ringed seals initiated their offshore trips (see Table 2). A 60 kg body mass was chosen since both male and female ringed seals are sexually mature at approximately this size (Lydersen and Gjertz, 1987). In addition to using two different scenarios for blubber mass gain at the ice edge (constant gains and decreased gains from day 60), we also simulated various scenarios for the location of the ice edge with a maximum distance located 900 km from the starting point of the trips in Svalbard. Note that the linear (orthodromic) distance between the North Pole and the north and south of Svalbard is approximately 1050 km and 1500 km respectively. In order to evaluate the sensitivity of the models to the assumed coastal blubber mass gain used (0.361 kg/day), we also ran different scenarios of

blubber mass gain for the seals that stayed in coastal areas during the whole period (0.5 kg/day and 0.2 kg/day, instead of 0.361 kg/day).

3. Results

3.1. Habitat use predictions

Based on the seafloor depths (bathymetry), distances to the nearest glacier front, distances to the coast and time in the year, Fig. 1 shows habitat use predictions for ringed seals in the coastal waters of Svalbard in August and December. Habitat use predictions are given as probabilities of being in the surrounding 10 km for 24 h or more. As expected from the coefficients in Table A1, higher probabilities are observed at shallow depths, close to glacier fronts and later in the season.

Taking into account the environmental variables that effect ringed seal habitat use offshore (in addition to inshore), Fig. 2 shows the predicted habitat use intensities in August for a larger area around Svalbard, under various scenarios of sea ice conditions. Habitat use intensity predictions are given as probabilities of being in the surrounding 30 km for 72 h or more. Since predictions were made separately using the inshore and the offshore CPH model, different probabilities were obtained in areas where sea ice made contact with the coasts of Svalbard. In those situations, the highest probability is presented, *i.e.* the maximum of the coastal or offshore model values for that pixel were used.

3.2. Blubber mass gain modelling

The expected blubber mass gained by a ringed seal travelling to the ice edge changed with distance to the edge and time spent there (Fig. 3). Simulation in Fig. 3A is for a ringed seal starting an offshore foraging trip on the 10th day of the 90 day simulation period (*i.e.*, 31st July; the average day that the tracked ringed seals initiated their offshore trips). Depending on the location of the ice edge, the maximum possible time spent there (given the fixed latest possible return date and the time spent in transit) will vary as depicted by the grey polygon in this figure. The thick green line illustrates the amount of time that this seal would have to spend at the ice edge in order to gain the same mass as if it had stayed at the coast during the whole simulation period. This amount of blubber (32.5 kg) could, for example, be obtained by spending 9 days at an ice edge located 100 km away or 18 days at an ice edge located 200 km from Svalbard (Fig. 3A) before returning to the coast and spending the rest of the simulation period there. If the ice edge is located too far away (more than 700 km and 630 km assuming constant or logistic growth, respectively) this seal would gain less mass than if it did not travel offshore at all. It should be noted that that continuous green line assumes that the daily blubber mass gain at the ice is 0.277 kg more than at the coast. The dashed green lines represent values using the S.E. of that value (0.277 ± 0.052 kg). Fig. 3A also shows scenarios for time spent at the ice edge at various distances; these result in mass gains above and below the "coastal" gain of 32.5 kg.
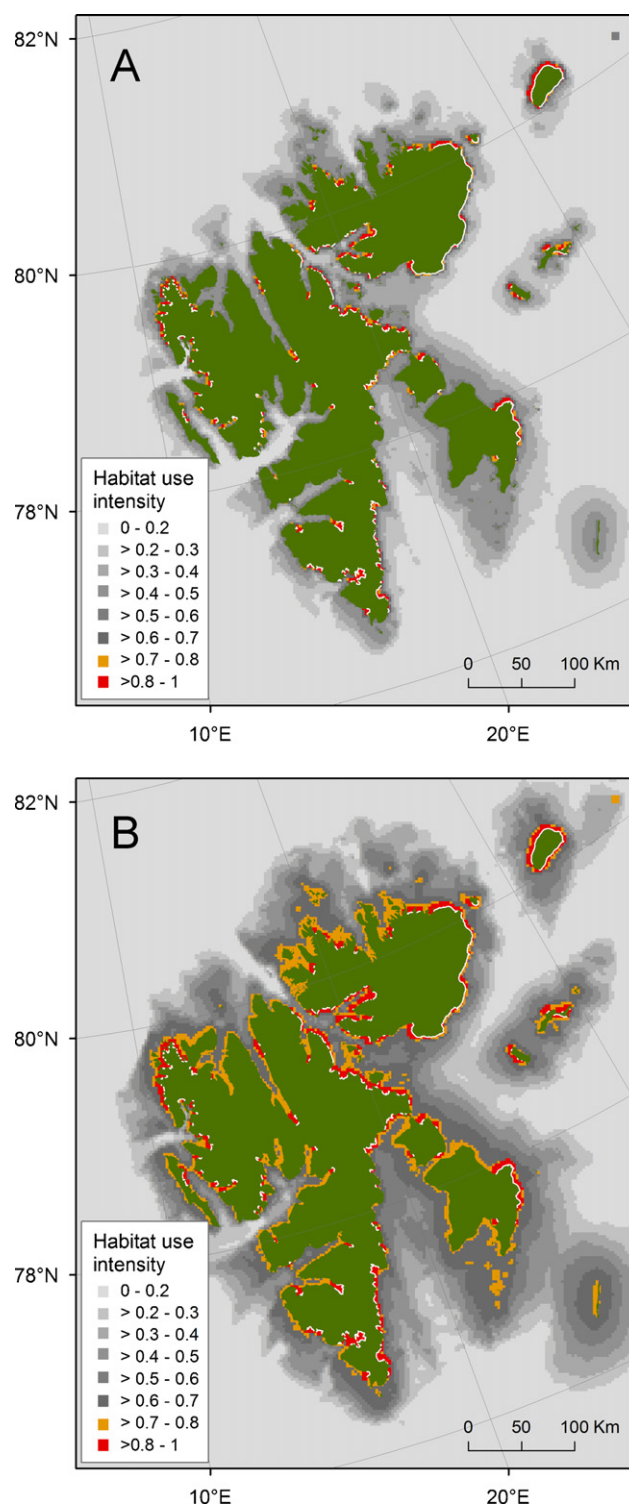

Fig. 1 – Predicted habitat use intensities for ringed seals in Svalbard presented as probabilities of being in the surrounding 10 km for more than 24 h. Predictions are given for August (A) and December (B) and are based on information on depth, distance to the nearest glacier front and distance to the coast from the central point of each grid. Grid size is 2.5 km. Glacier fronts are shown in white.
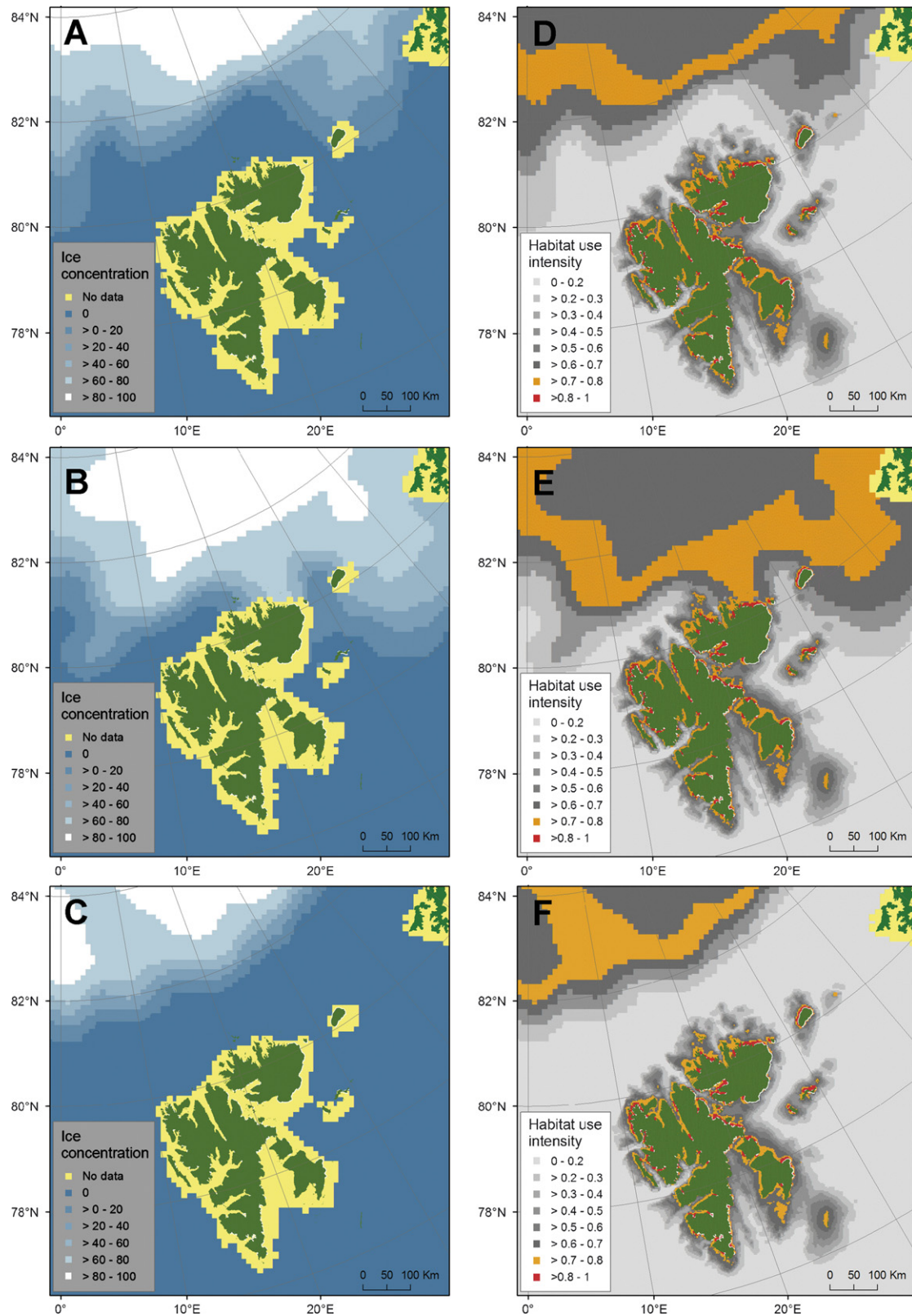
Fig. 2 – Predicted habitat use intensities, presented as probabilities of being in the surrounding 30 km for more than 72 h, for August (panels D, E and F), under various scenarios of sea ice conditions (shown in the panels on the left—panels A, B and C). Predictions were made using the inshore and the offshore model. In the locations where different probabilities were obtained from different models, the highest value is presented. Sea ice concentrations in the panels on the left correspond to real values observed on the 25th of August 2002 (A), 2003 (B) and 2004 (C). Areas with unknown ice conditions are plotted in yellow.
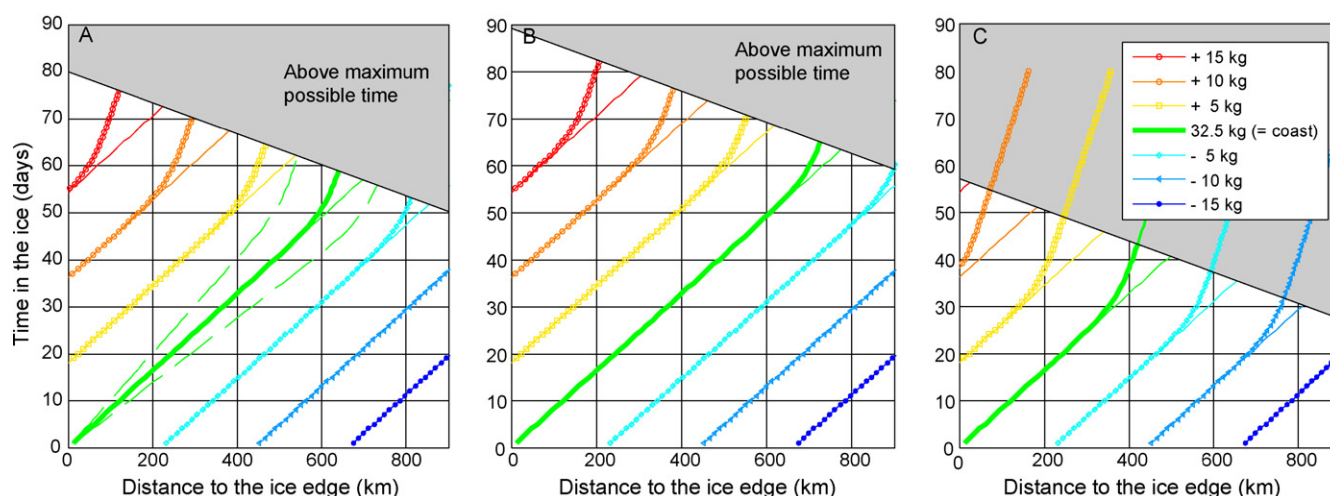
Fig. 3 – Blubber mass gain with a 90-day simulation period by a 60 kg ringed seal spending different amounts of time (y-axis) at an ice edge located at increased distances from Svalbard (x-axis). Simulations are given for a trip starting at day 10 (A), day 1 (B) and day 33 (C). The straight thin lines correspond to the assumption of a continuous blubber mass gain during the whole season. Thick lines correspond to the assumption of a logistic decrease in blubber mass gain from day 60 onwards. Simulations assume a daily blubber mass gain at the ice 0.277 kg higher than at the coast to compensate for the energy lost in transit. Dashed green lines in panel A are created using the S.E. of that value (0.277 ± 0.052 kg).

When starting a trip at the earliest date (day 1, July 22nd), the maximum distance ringed seals could travel between their start point in Svalbard and the ice edge and still gain the same amount of blubber as if they stayed at the coast is increased to 700–750 km (Fig. 3B). The corresponding distance for the latest departure date (August 23rd) would be reduced to 400–500 km (Fig. 3C). Travel to ice edges beyond these distances would result in a lower mass gain than if ringed seals had stayed at the coast the whole time.

When using coastal blubber mass gains of 0.2 kg and 0.5 kg respectively (instead of 0.361 kg/day from Ryg et al., 1990), the extra daily mass gains at the ice edge for the seals that move offshore would then be 0.201 ± 0.039 kg and 0.342 ± 0.064 kg, respectively (instead of 0.277 ± 0.052 kg). However, about the same number of days is needed at the ice edge to gain the same amount of blubber as at the coast irrespective of the variation in the daily mass gain values (Fig. 4). In addition, as long as the seals that travel gain the same amount of blubber as those that stay along the coast, whatever this mass value is, the maximum distance to the ice edge cannot exceed 600–700 km (Fig. 4).

4.   Discussion

This is the first time that survival functions (*i.e.*, here first passage time functions) from CPH models are used to make cartographic predictions of a species' habitat use. These spatial predictions can have several applications. They can aid reserve selection; serve as a basis for assessments of the likelihood of interference between seals and factors such as tourist traffic and oil spills; or to evaluate the likely impacts of environmental changes, such as alterations in sea ice conditions (as illustrated in this study).

Cartographic predictions do not quantify the effect of the model variables (environmental variables) on animal's space use. This is done by the explanatory model (the hazard function in this case). No novel information on the relationship between an animal's behavior and environmental variables are provided by this type of illustration. But, this does provide a means to visualize an extrapolation of the model parameters for new areas. This makes cartographic predictions particularly valuable for model checking (for validating the models underlying the predictions) and as a basis for making model improvements. In the present study, the physical variables included in the coastal and offshore models explained a large proportion of the variability in the data (36% and 58% for the best coastal and offshore model respectively; see Freitas et al., 2008). However, there is still a considerable amount of variability in the data that is not related to these explanatory variables. There is for instance no information included in the analyses on ice conditions in coastal waters since available satellite data cannot provide this feature for coastal pixels where observations might be contaminated by land (Andersen et al., 2007). This variable, and in particular the presence of land-fast ice inside the fjords, is expected to greatly reduce the tendency for leaving exhibited by ringed seals. Although this was in part reflected by reduced risk of leaving as winter approached, presence/absence data for fast ice would be an extremely important variable to include in future models; this feature is known to be important to ringed seal breeding biology (McLaren, 1958; Lydersen and Gjertz, 1986).

Another uncertainty in the models presented relates to habitat use intensities for offshore ringed seals that penetrate deep into the ice. None of the tracked seals moved further into this habitat than 272 km from the southern edge (mean ± S.E. was 110 ± 1.7 km, n = 1211 observations). For these seals occu-
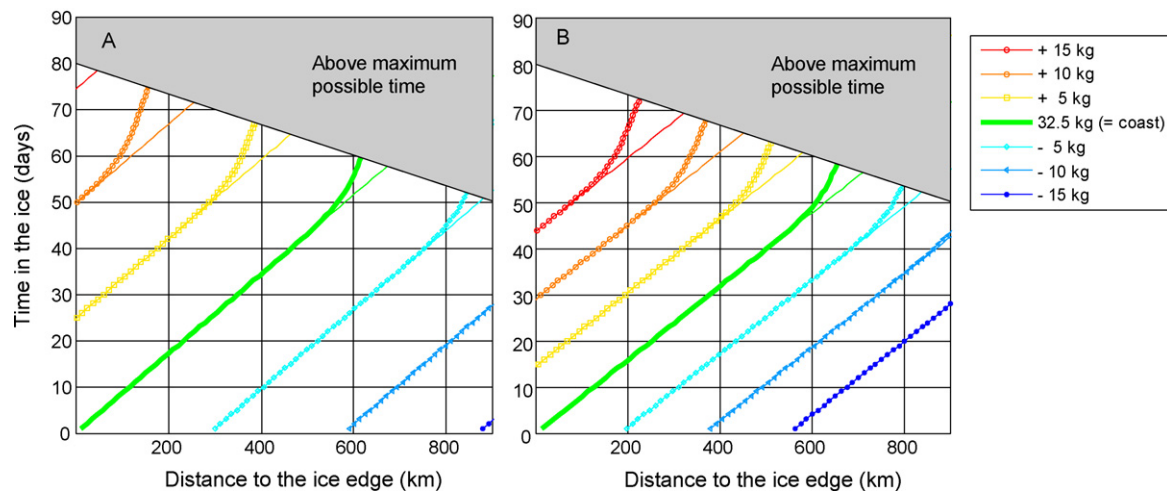
Fig. 4 – As in Fig. 3, but assuming different values for the average blubber mass gain at the coast: 0.2 kg/day (A), and 0.5 kg/day (B). Straight thin lines correspond to the assumption of a continuous blubber mass gain during the whole season. Thick lines correspond to the assumption of a logistic decrease in blubber mass gain from day 60 onward.

pying areas with 80–100% ice concentration, constant habitat use intensities are used in the models, while this parameter likely will decrease with increasing distance from the ice edge. However, since no data are available for quantifying this potential decrease, this value is kept constant in the current modelling effort.

The location of the offshore ice is another parameter that may affect the models in a different way than predicted in the present study. Distance between the offshore ice edge and the coastal tagging location did not affect FPTs for the instrumented ringed seals during the 2 years of tracking presented in Freitas et al. (2008). However, it is possible that the seals will respond to an increase in this distance by changing their FPTs both during transit and during their stay in the offshore ice areas if the ice edge position is very different from the conditions observed during the 2 years that formed the basis for the parameterization of the models.

The summer sea ice extension has been declining since the 1970s in many parts of the Arctic with the largest changes occurring in the Beaufort, Chukchi, Siberian, Laptev and Kara Seas (Comiso, 2002; Stroeve et al., 2005, 2007; Francis and Hunter, 2006; Christensen et al., 2007; Comiso et al., 2008). A decrease rate of 9–10% per decade has been observed for the Arctic in general (Comiso, 2002; Stroeve et al., 2007; Comiso et al., 2008). Analyses of tracking data from the ringed seals used in this study indicates that no significant feeding takes place during transit from the coast to the offshore ice edge (see Freitas et al., 2008). It is probably not energetically profitable to search for relatively less predictable patches of food along the route, since the ice edge is such a predictable hot spot for aggregations of prey for this seal species (see Engelsen et al., 2002). A logical consequence of this behavior is that there will be a given distance to the location of the ice edge above which the cost of transit will exceed the energy gained there. This study predicts that an ice edge located further away than about 600–700 km from the starting point of the trip in Svalbard represents a critical distance; and if the seals initiate their

movements as late as the latest of the study animals (August 23rd), this critical distance is reduced to about 400 km from the archipelago (from the start point of the trip, which is not necessarily in the north of Svalbard).

If the sea ice retreats further than the critical distance identified in this study, it may have severe consequences for the ringed seal population in Svalbard. Fat seals are healthy seals with good reserves, and a reduced blubber mass gain during summer would almost certainly manifest itself in decreased animal fitness via a decrease in reproductive rates or general survival. One potential coping mechanism if the migration distance became too long would obviously be to cease travelling to the northern ice edge. Note that only about 50% of the tracked seals travelled to the sea ice edge in summer (Freitas et al., 2008). However, if all ringed seals stayed coastally throughout the year, increased intraspecific competition would almost certainly be a result. The areas in front of glaciers that protrude out into the ocean and create hot spots for ringed seal prey (see Hop et al., 2002) are not likely extensive enough to sustain the present ringed seal population in Svalbard (see Smith and Lydersen, 1991; Krafft et al., 2006). Thus, a population decline would almost certainly result from density-dependent processes. An additional complication for ringed seals is the fact that the same climatic factors responsible for reducing the summer sea ice extension are also responsible for glaciers currently receding in Svalbard (as can be observed in Norwegian Polar Institute maps; see also Kohler et al., 2007). If the productive glacier front areas disappear in the future, fish and invertebrate populations may become more dispersed and hence less energetically profitable for top predators, even if they maintain, or even increase, current abundance/biomass levels. Thus, the changes that are taking place in the Arctic are likely to have very far-ranging consequences for ringed seals and their behavior on an annual cycle, not just during the current summer open water period.

An input parameter to the model that should be considered with some caution is the daily mass gain from Ryg et

al. (1990), which is based on very few individuals ($n = 7$). However, it should be noted that the model is relatively insensitive to variation in the daily mass gain values ($\pm 40\%$). Approximately the same number of days is needed at the offshore edge independent of the daily mass gain value as long as we assume that the ringed seals that travel off shore should come back in the same condition as those that stayed in coastal areas.

One input parameter that was kept constant in this modelling exercise is the return date; *i.e.*, the time when the seals have to be back in the fjords of Svalbard before the fast-ice formation starts. In a future, warmer climate scenario, it is a possible that this date will occur later and later in the year, thus giving the seals the possibility for a prolonged period in the offshore ice compared with what is modelled above; this would contribute positively to the seal's annual energy budget (perhaps compensating somewhat for the distance issue). Of course, the growth season will not increase indefinitely in the Arctic because algal production is minimal during the polar night, and this will not change regardless of warmer temperatures. An extreme coastal sea ice scenario, that was difficult to envisage just a few years ago, where fast-ice formation in Svalbard does not occur at all, in fact happened for the west coast of Spitsbergen, Svalbard in 2006 and 2007 (CF, KMK, CL, personal observation). If this situation becomes a norm, with no annual land-fast ice within the fjords of the archipelago, ringed seals will either have to change their breeding behavior dramatically (a long term evolution) or at least leave the coastal breeding areas and retreat to offshore pack-ice exclusively, reducing their range and presumably also their reproductive success rates. Ringed seals are known to be able to breed in offshore pack-ice (Finley et al., 1983; Wiig et al., 1999), however, the most preferred breeding habitat is stable land-fast ice (McLaren, 1958; Furgal et al., 1996), such as occurs in the fjords of Svalbard today (Lydersen and Gjertz, 1986; Smith and Lydersen, 1991). An absence of sea ice (both pack- and fast-ice) from Svalbard will also affect the local densities of polar cod and other important prey species for ringed seals. The replacement of these lipid-rich prey types by less-lipid-rich, temperate, species could be problematic for arctic marine predators such as ringed seals that depend on rapid accumulation of energy to restore blubber stores during the short season of productivity at high latitudes (see Trites and Donnelly, 2003; Rosen and Trites, 2005; Blachowiak-Samolyk et al., 2007; Steen et al., 2007; Kovacs and Lydersen, 2008). Declines in the productivity rates at ice edges if the annually formed northern ice cap does not come south far enough to occur over shelf areas is another serious concern for some ice-dependent marine mammals (see Laidre et al., 2008). In addition, a warmer climate will likely lead to invasions by more temperate seal species into the north, that will compete with ringed seals for resources. Potential increases in predation rates by killer whales and other predators that are currently unable to inhabit arctic waters may also be an issue for ringed seals, though reductions in polar bear predation may be compensatory in this regard (Tynan and DeMaster, 1997; Learmonth et al., 2006; Kovacs and Lydersen, 2008). However, predictions of these latter scenarios are outside the scope of this study.

In summary, this study has shown that survival functions derived from CPH models can be used for dynamic predictions of animal space use. These dynamic predictions (in space and time) can have wide applications for studies of other marine and terrestrial species that are based on data collected from telemetry. Although predictions of high habitat use intensities could be made, these predictions cannot readily be extrapolated to very different ice conditions. Indeed modelling the energetics of seal migrations to the ice edges indicate that summer foraging migrations are expected to become energetically unprofitable if the sea ice retreats further than 600–700 km from Svalbard.

Acknowledgements

Appendix A

See Tables A1–A3.

Table A1 – Estimated coefficients (β), hazard ratios (e^{β}), standard errors (S.E.(β)) and significance levels (P) of the CPH model that best describes the risk or tendency of leaving by ringed seals in inshore waters of Svalbard

Variable	β	e^{β}	S.E.(β)	P
Glac [0–5 km]	–	–	–	–
Glac [>5–10 km]	0.614	1.848	0.043	<0.001
Glac [>10–20 km]	1.188	3.281	0.056	<0.001
Glac [>20 km]	1.279	3.594	0.047	<0.001
Coast	0.018	1.019	0.004	<0.001
Depth	0.005	1.005	0.001	<0.001
Month [August]	–	–	–	–
Month [September]	0.101	1.106	0.039	0.010
Month [October]	0.062	1.064	0.041	0.120
Month [November]	−0.297	0.743	0.052	<0.001
Month [December]	−0.716	0.489	0.061	<0.001

The model was fitted using first-passage times (FPT) for a radius of 10 km as survival times. Note that a hazard ratio (e^{β}) lower than one for an X variable indicates a decreased risk of leaving. A hazard ratio (e^{β}) higher than one is interpreted in the opposite way. The percentage of the variability in the data explained by the model was 35.6%. *Source*: Freitas et al. (2008).
Model abbreviations: Glac is distance to nearest glacier front; Coast is distance to the coast (km); Depth is sea bottom depth (m); and Month is the calendar month.

Table A2 – Same as above (Table A1), but with the CPH model fitted using first-passage times (FPT) for a radius of 30 km as survival times

Variable	β	e^{β}	S.E.(β)	P
Glac [0–5 km]	–	–	–	–
Glac [>5–10 km]	0.350	1.419	0.043	<0.001
Glac [>10–20 km]	0.413	1.511	0.053	<0.001
Glac [>20 km]	0.787	2.196	0.045	<0.001
Coast	0.017	1.017	0.004	<0.001
Depth	0.008	1.008	0.001	<0.001
Month [August]	–	–	–	
Month [September]	−0.016	0.984	0.039	0.680
Month [October]	−0.123	0.884	0.040	0.002
Month [November]	−0.572	0.564	0.052	<0.001
Month [December]	−0.890	0.411	0.061	<0.001

The percentage of the variability in the data explained by the model was 30.4%. Note that no coefficients are presented for the first distance to glacier (Glac) and time in the year (Month) category, since these are the base levels used for comparison.
Model abbreviations: Glac is distance to nearest glacier front; Coast is distance to the coast (km); Depth is sea bottom depth (m); and Month is the calendar month.

Table A3 – Estimated coefficients (β), hazard ratios (e^{β}), standard errors (S.E.(β)) and significance levels (P) of the CPH model used to describe the risk of leaving by ringed seals in offshore waters of Svalbard

Variable	β	e^{β}	S.E.(β)	P
Conc [0]	–	–	–	–
Conc [>0–20]	−0.29	0.75	0.09	0.001
Conc [>20–40]	−0.83	0.44	0.08	<0.001
Conc [>40–60]	−1.52	0.22	0.08	<0.001
Conc [>60–80]	−1.71	0.18	0.09	<0.001
Conc [>80–100]	−1.44	0.24	0.13	<0.001
Month [August]	–	–	–	–
Month [September]	0.24	1.28	0.07	<0.001
Month [October]	0.63	1.87	0.11	<0.001
Month [November]	1.40	4.07	0.14	<0.001

The model was fitted using first-passage times (FPT) for a radius of 30 km as survival times. Note that a hazard ratio (e^{β}) lower than one indicates a decreased risk of leaving. A hazard ratio (e^{β}) lower than one is interpreted in the opposite way. The percentage of the variability in the data explained by the models was 29.6%.
Model abbreviations: Conc is sea ice concentration in %; and Month is the calendar month.

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